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THE INFLUENCE OF HABITAT AND FISHING ON REEF FISH ASSEMBLAGES IN CUBA

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ABSTRACT: The abundance of selected fish species was estimated using the stationary visual census technique in the northwestern region of the Cuban shelf. A total of 26,809 individuals of 32 species were counted in 1,172 stationary point censuses made at 10 reef sites along the coast. We found that the abundance patterns were most probably the consequence of the presence/absence of mangroves and seagrass beds in adjacent lagoon areas. A second factor influencing the spatial variation appeared to be overfishing on an east-west gradient, with lower abundances of commercially targeted species near Havana City in the east.

RESUMEN: La abundancia de especies de peces seleccionadas fue estimada usando una técnica de censo visual estacionario en la región noroccidental de la plataforma cubana. Se realizaron 1,172 censos puntuales estacionarios en 10 sitios arrecifales a lo largo de la costa. Se contaron en total 26,809 individuos pertenecientes a 32 especies. Se encontró que los patrones de distribución de abundancia son muy probablemente la consecuencia de la presencia o no de manglares y pastizales marinos en las áreas lagunares adyacentes. Un segundo factor que influye en la variación espacial parece ser un gradiente de sobrepesca en la dirección este-oeste, con abundancias menores de peces comerciales cerca de la Ciudad de La Habana, en el este.

INTRODUCTION

The function of mangroves and seagrass beds as nursery areas for coral reef fishes is well established (Heck et al. 2003, Mumby et al. 2004, Adams et al. 2006). The processes and mechanisms of connectivity from the back reef, e.g., mangroves and lagoons, across seagrass beds to the fore reef have been reviewed by several authors (Beck et al. 2003, Hughes et al. 2005, Sale et al. 2005, Cowen et al. 2006). At the species level, it is clear that there are more questions than answers about the function of backreef zones for coral reef fishes. Some species appear to be strongly dependent on seagrass and mangrove habitats (Nagelkerken et al. 2002, Dorenbosch et al. 2004), while other findings caution against a generalized hypothesis that back reefs are nursery habitats (Chittaro et al. 2005, Dorenbosch et al. 2007). There is some debate whether back-reef habitats significantly contribute to the fish population of the coral reef or only function as additional habitats (Beck et al. 2003, Heck et al. 2003).

One challenge is our inability to clearly define nursery habitats for coral reef fishes (Dahlgren et al. 2006, Sheaves et al. 2006, Layman et al. 2006). Based on visual census data in different habitats, Nagelkerken et al. (2002) suggested just 4 species heavily dependent on lagoons as nurseries. Seven additional species used the lagoon, but there was insufficient evidence to classify the lagoon as a nursery area. Dorenbosch et al. (2004) suggested that some species are highly dependent on the presence of bays with seagrass beds and mangroves as nurseries at the scale of whole islands.

Mangrove habitats can be obligate nursery areas for the rainbow parrot fish, *Scarus guacamaia*, (Dorenbosch et al. 2006), and adult densities can be significantly greater at reefs with adjacent mangroves (Mumby et al. 2004).

In contrast, Chittaro et al. (2005) found that only 4 of the 6 most abundant and commercially important species (*Haemulon flavolineatum*, *H. sciurus*, *Lutjanus apodus* and *L. mahogoni*) showed higher numbers of juvenile fish in mangrove and/or seagrass habitats with adjacent coral reefs, and at just 4 of 9 sites studied. Dorenbosch et al. (2007) found that most fish species using seagrass and mangroves as juvenile habitats were absent from, or showed reduced densities on adjacent, but distant coral reefs (> 9 km away). They proposed that seagrass and mangrove areas should not be generalized as juvenile habitats because habitat configuration, e.g., distance between, may limit connectivity between mangroves, seagrass beds, and coral reefs.

In a recent review, Adams et al. (2006) classified coral reef fishes based upon their inter-habitat, ontogenic migration patterns. The authors define Group A as habitat specialists using the same habitat at all life stages, Group B as habitat generalists which are not site-attached and use a variety of habitats, and Group C as ontogenetic shifters. The latter species switch habitats during their life, such as the transition from settlement to juvenile to maturing adults. Habitat connectivity from back to fore reef is predicted to be critical for such species. Results by Gratwicke et al. (2006) showed that a detailed review of the natural life-history strat-

Figure 1. Northwestern region of Cuban shelf. *a.* Western portion; *b.* Eastern portion. Open circles indicate studied reef areas.

egies and habitat requirements are required before making further generalizations about the role of nearshore habitat types as nurseries for reef fishes.

From 1996 to 2006, the fish assemblages and habitats of northwestern Cuba have been investigated (Aguilar et al. 1997, Gonzalez-Sanson et al. 1997, Aguilar et al. 2004, Guardia et al. 2005). We re-examined these data in relation to the potential habitat connectivity within reef complexes along the coast, and discuss how species complexes are organized by the degree of potential connectivity. In addition, a pollution gradient along this coast (Aguilar et al. 2007), in conjunction with probable overfishing, may influence fish assemblages. These latter factors are incorporated into our observations and discussion.

MATERIALS AND METHODS

Study Area

The study was conducted in the northwestern region of the Cuban shelf. The main shallow-water habitats in this region are fringing coral reefs, seagrass beds and nearshore mangrove prop-root muddy environments. The estimated

total surface area of this shelf region, which extends from the high tide line to the 200 m isobath, is 4,050 km². Mean shelf depth is 4-5 m, although at some locations in the Gulf of Guantánamo the depth can be up to 18 m (Figure 1). Reefs included in the study are defined in Table 1.

At Havana City in the east, a frontal fringing reef develops mainly in the 12-15 m deep terrace, at 200-300 m offshore. The area between the shore and the reef is an almost bare rocky plain. Since the impact of pollution coming from the city varies notably along the coast from Havana harbor entrance (most polluted area) towards the southwest, the reef was divided in three different sites named HC1, HC2 and HC3, and analyzed separately. More details and the rationale for this division can be found in Aguilar et al. (2004) and Aguilar et al. (2007).

Baracoa (B) is a fringing reef near a small town of the same name. The reef has a well developed crest (length = 1 km) dominated by *Acropora palmata* and a small seagrass bed (< 4 ha) in the lagoon. The shoreline is highly modified by man-made structures and no mangrove growth is present. A heavily polluted small coastal lagoon (ca. 20 ha) near this reef has a small mangrove growth (< 1 ha). La Herradura (LH) is a fringing reef growing on the west side of a cove of the same name. It has a poorly developed crest dominated by *A. palmata* and a well developed, but small seagrass bed in the lagoon (< 2 ha). The shore is a sandy beach with no mangroves. Cayo Levisa (CL) is the reef of the key with the same name. It has a poorly structured crest dominated by *A. palmata* and a well-developed seagrass bed in the backreef zone. Mangroves are very abundant in the southern shore of the key and along the mainland. The Los Colorados reef (LC1 to LC4) is a large bank-barrier reef (length ~ 40 km with a wide crest area of *A. palmata*). Significant expanses of seagrass beds in the lagoon (more than 500 km²) abut well developed mangroves along the shore (length of coast with mangrove ~ 80 km).

Levels of pollution and fishing pressure were defined for each reef (Table 1). Two rank scales were prepared based on anecdotal information, geographic position of the reefs in relation to main pollution sources, and distance to urban centers. These scales are defined as follows:

Pollution:

1. Very low. Reefs which are very far (> 30 km) from any urban center or land-based pollution source. No evidence of any contamination.
2. Low. Reefs which are far from any urban center or industrial waste source, but not far from the coast. Some pollution from agriculture is assumed in this case.
3. High. Reefs which are near the coast in narrow shelf areas adjacent to big urban centers but without the direct impact of big discharges.
4. Very high. Reefs which are near the coast in narrow shelf areas adjacent to big urban centers and are receiving the

TABLE 1. Geographical position, associated lagoonal habitats, sampling dates and sizes, pollution levels and fishing impact of the studied reefs (see also Figure 1 and text for details).

Reef	Reference coordinates	Lagoon habitats	Sampling dates	Number of censuses	Pollution ^A level	Fishing ^B impact
HC1	23° 08.549' N 82° 22.012' W	Rocky plain	Feb-Mar 2000	96	4	3
			Jun 2000	96		
HC2	23° 08.250' N 82° 24.565' W	Rocky plain	Feb-Mar 2000	64	3	3
			Jun 2000	64		
HC3	23° 07.359' N 82° 26.087' W	Rocky plain	Feb-Mar 2000	80	3	3
			Jun 2000	80		
B	23° 03.362' N 82° 335.97' W	Seagrass bed	April 2004	99	2	2
			September 2004	99		
LH	23° 01.481' N 82° 55.014' W	Seagrass bed	March 1996	108	2	2
			October 1996	109		
CL	22° 52.890' N 83° 34.093' W	Seagrass bed & mangrove	June 2003	27	2	2
			October 2003	70		
LC1	22° 23.023' N 84° 36.589' W	Seagrass bed & mangrove	March 2006	45	1	1
LC2	22° 18.320' N 84° 40.235' W	Seagrass bed & mangrove	March 2006	45	1	1
LC3	22° 13.970' N 84° 44.091' W	Seagrass bed & mangrove	March 2006	45	1	1
LC4	22° 09.451' N 84° 46.373' W	Seagrass bed & mangrove	March 2006	45	1	1

A: 1-very low; 2-low; 3-high; 4-very high. B: 1-high; 2-very high; 3-exceedingly high.

direct impact of big pollution discharges (e.g. tidal discharge from a heavily polluted port).

Fishing pressure:

1. High. Reefs which are very far (> 30 km) from any urban center. Only commercial vessels fish in these reef areas and target species are big-sized species (e.g., larger snappers, groupers, jacks).
2. Very high. Reefs which are far from any urban center but near small coastal villages. Almost no commercial fishing and heavy subsistence fishing pressure mostly with small boats.
3. Exceedingly high. Reefs which are near the coast in narrow shelf areas adjacent to big urban centers. A very high

subsistence fishing effort by people using small rafts, boats, spearguns, gill nets with small mesh size and traps.

Sampling Procedures

In all reefs but Los Colorados, sampling occurred on two different dates. In these cases data of each sampling date were treated as separate units in our analyses (Table 1).

The abundance of fish was estimated using the stationary visual census technique of Bohnsack and Bannerot (1986) with some minor modifications. The nominal radius of the observing cylinder was 5 m. As the fish assemblage composition can vary substantially between different biotopes within a reef (crest, spur & grooves, terrace, etc.), we made repeated censuses in each main biotope at each reef. Counts

TABLE 2. Mean, minimum and maximum abundance estimations, frequency of occurrence (F) in the 16 samples and total length (TL) range of fish counted for each species included in the study. Rank-correlation values (r_s) were calculated between species abundance at each site and rank of sampling sites along the coast from west to east. Probabilities (p) for r_s values which are significant are in bold.

Species	Individuals per count			F	TL (cm)	r_s	p
	Mean	Min	Max				
<i>Cephalopis cruentata</i>	0.15	0.00	1.37	11	14 - 20	0.24	0.365
<i>Cephalopis fulva</i>	0.47	0.02	2.16	16	10 - 25	0.64	0.007
<i>Epinephelus ascensionis</i>	0.02	0.00	0.13	5	20 - 30	0.58	0.018
<i>Epinephelus guttatus</i>	0.13	0.00	1.31	12	15 - 40	0.64	0.007
<i>Epinephelus striatus</i>	0.02	0.00	0.11	6	30 - 60	0.80	< 0.001
<i>Lutjanus analis</i>	0.05	0.00	0.27	10	40 - 75	0.29	0.273
<i>Lutjanus apodus</i>	0.35	0.00	1.00	11	15 - 40	0.61	0.012
<i>Lutjanus cyanopterus</i>	0.02	0.00	0.29	5	40 - 60	0.76	0.001
<i>Lutjanus synagris</i>	0.29	0.00	1.15	10	15 - 25	-0.83	< 0.001
<i>Ocyurus chrysurus</i>	0.46	0.00	1.73	14	15 - 30	0.14	0.616
<i>Gerres cinereus</i>	0.05	0.00	0.15	9	15 - 20	-0.57	0.020
<i>Haemulon aurolineatum</i>	0.28	0.00	3.59	6	10 - 15	-0.27	0.315
<i>Haemulon carbonarium</i>	0.10	0.00	0.86	7	10 - 15	-0.76	0.001
<i>Haemulon chrysargyreum</i>	0.30	0.00	1.60	9	10 - 15	0.17	0.522
<i>Haemulon flavolineatum</i>	2.27	0.30	5.54	16	10 - 20	-0.44	0.084
<i>Haemulon plumieri</i>	1.01	0.08	3.16	16	10 - 25	0.29	0.272
<i>Haemulon sciurus</i>	0.46	0.04	1.19	16	10 - 25	0.39	0.134
<i>Chaetodon capistratus</i>	1.00	0.20	2.07	16	8 - 17	-0.32	0.224
<i>Chaetodon ocellatus</i>	0.22	0.00	0.45	15	12 - 18	-0.69	0.003
<i>Chaetodon sedentarius</i>	0.15	0.00	0.70	11	10 - 15	-0.73	0.001
<i>Chaetodon striatus</i>	0.45	0.07	2.18	16	8 - 15	0.20	0.459
<i>Lachnolaimus maximus</i>	0.03	0.00	0.24	5	25 - 40	0.70	0.002
<i>S. iseri /taeniopterus</i>	2.92	0.18	15.43	16	5 - 30	0.85	< 0.001
<i>Sparisoma atomarium</i>	0.19	0.00	2.09	7	3 - 12	0.87	< 0.001
<i>Sparisoma aurofrenatum</i>	1.17	0.02	5.01	16	10 - 30	0.14	0.612
<i>Sparisoma chrysopetrum</i>	0.24	0.00	0.97	14	10 - 30	0.01	0.965
<i>Sparisoma rubripinne</i>	0.39	0.00	2.03	15	15 - 30	0.16	0.548
<i>Sparisoma viride</i>	1.11	0.09	4.49	16	15 - 30	0.86	< 0.001
<i>Acanthurus bahianus</i>	5.01	0.96	9.68	16	10 - 25	-0.60	0.014
<i>Acanthurus chirurgus</i>	0.62	0.00	1.94	14	13 - 25	-0.76	0.001
<i>Acanthurus coeruleus</i>	2.90	0.93	7.55	16	10 - 25	0.34	0.192
<i>Sphyrna barracuda</i>	0.07	0.00	0.44	8	65 - 120	0.83	< 0.001

per biotope were pooled for each reef (Table 1). Data are given as mean number of individuals per census.

Original data included all species observed. For the present analyses, not all species or groups of species (families and/or genera) were selected. We excluded Adams et al.'s (2006) habitat specialists and generalists (Groups A and B, e.g. damselfishes and small wrasses, respectively). Nocturnal species were also excluded as they are highly cryptic during the day. Species included were the families Acanthuridae, Scaridae, Lutjanidae, Serranidae (genera *Epinephelus* and *Mycteroperca*) and Chaetodontidae. Three additional species which have been considered habitat-shifters were also included: *Sphyrna barracuda*, *Lachnolaimus maximus* and *Gerres cinereus*. The species *Scarus iseri* and *S. taeniopterus* were usually indistinguishable in the field and we hereafter refer to them as *S. iseri/taeniopterus*.

Statistical Analysis

Hierarchical agglomerative cluster analyses were per-

formed using as dissimilarity measures the Bray-Curtis distance on fourth-root transformed counts for samples grouping and $1-r_s$ (r_s = Spearman's rank correlation coefficient) for inverse analysis (clustering species; Boesch 1977). In all cases the UPGMA clustering algorithm was used. Non parametric multidimensional scaling (MDS) was employed for ordination of samples based in same distance matrices as cluster analyses. The combination of clustering and ordination analysis has been described by Clarke and Warwick (2001) as the most effective way to check the adequacy and mutual consistency of both representations. One-way ANOSIM (Clarke and Warwick 2001) was used to verify the significance in fish assemblage composition of samples classified *a priori* by the presence/absence of seagrass and/or mangrove. All analyses were made using PRIMER 5.5 and STATISTICA 6.0 software.

As a complement to Cluster and ANOSIM analyses, rank correlation coefficients were calculated between the abun-

dance of each species and the ranks of sites according to their position along the coast (rank 1 for HC1 to rank 10 for LC4 - see Table 1). In this analysis, species more abundant towards the east will have significant negative coefficient values and those more abundant towards the west will have significant positive coefficient values.

RESULTS

A total of 26,809 individuals of 32 species of the selected groups were counted in 1,172 stationary point censuses (Table 2). The most abundant species were the medium-sized herbivores *A. bahianus*, *A. coeruleus*, *S. iseri/taeniopterus* complex, *S. aurofrenatum* and *S. viride*, and the medium sized small-invertebrates feeders *H. flavolineatum* and *H. plumieri*. Only two species of higher trophic levels were abundant enough to be included: *E. striatus* and *S. barracuda*.

All the species of *Mycteroperca* spp. (large groupers) were extremely scarce and were not included in further analyses. Larger herbivores were also rare; two individuals of *Scarus coelestinus* were observed and no *S. coeruleus* or *Scarus guacamaia* were observed.

After the numerical classification and multidimensional scaling, samples formed three well separated groups (Figure 2). Group A included all the sites off Havana City. Group B included samples at Baracoa and La Herradura reefs. Group C was in the Levisa key and Los Colorados reefs. Groups correlated well with the presence or absence of seagrass beds and/or mangroves in the lagoon, the fishing pressure levels and pollution levels (Table 1).

ANOSIM based on presence/absence of seagrass or mangrove produced a global test that was significant ($R = 0.962$, $p = 0.001$). The pairwise comparisons were also significant ($R_{A,B} = 0.960$, $p = 0.005$; $R_{A,C} = 0.981$, $p = 0.002$; $R_{B,C} = 0.960$, $p = 0.005$). This pre-determined classification coincides with the results of hierarchical classification and ordination methods.

Two well differentiated groups of species were obtained (Figure 3). The first group included all species of the genus *Acanthurus*, the majority of species in genera *Haemulon* and *Chaetodon*, *G. cinereus* and one species each of Lutjanidae and Scaridae. The second group includes all species in genus *Epinephelus*, the majority of species in the families Lutjanidae and Scaridae, *S. barracuda*, *L. maximus* and just two species of the genus *Haemulon* and one of the genus *Chaetodon*.

Of the 32 species included in the study, 18 showed significant correlation with the ordering of sites (Table 2). Some correlations were negative, indicating increase of abundance towards the east. This was the case for *A. bahianus*, *A. chirurgus*, *C. ocellatus*, *C. sedentarius*, *G. cinereus*, *H. carbonarium* and *L. synagris*. Other correlations were positive indicating increase of abundance towards the west. This was the case for *E. ascensionis*, *E. guttatus*, *E. striatus*, *L. apodus*, *L. cyanopterus*,

S. iseri/taeniopterus, *S. atomarium* and *S. barracuda*.

A joint plot of abundances for species which showed significant correlation revealed a clear pattern (Figure 4) that explained site clustering (Figure 2): Group A is dominated by species which are more abundant in the east; Group C includes mainly species most abundant in the west; and Group B is defined by species which have similar abundances across the entire coast. A more detailed comparative analysis by species gives a better understanding of the patterns observed.

The surgeonfishes, *A. bahianus* and *A. chirurgus*, showed a high correlation in their abundances ($r_s = 0.804$, $p = 0.0002$) while both had a weak correlation with *A. coeruleus*, i.e., the first two species were more abundant towards the east, while *A. coeruleus* showed no significant trend in its abundance. Similarly, *C. ocellatus* and *C. sedentarius* were highly correlated ($r_s = 0.931$, $p < 0.0001$). These species were significantly more abundant toward the east and had no significant correlation with other species in the genus. The abundance of two grunts, *H. flavolineatum* and *H. chrysargireum* behaved in the same fashion, as they were highly correlated ($r_s =$

Figure 2. Classification (upper panel) and MDS ordination (bottom panel) of samples. Each sample is identified by the acronym of the sampling reef area (capital letters and numbers) and the date (month) of sampling (lowercase letters). See Table 1 and Figure 1 for more details.

Figure 3. Classification of species included in the study.

0.604, $p = 0.013$) and showed no significant correlation with other species in the genus. They also significantly increased in abundance toward the east.

The abundances of small groupers (*Epinephelus* spp. and *Cephalopholis* spp.) were, in general, significantly correlated. All species but *C. cruentata* showed high positive correlation with site ranks, were more abundant towards the west, and were closely clustered (Figure 3). The same was true for the majority of parrotfishes (Scaridae) with the notable exception of *S. rubripinne* which was negatively correlated with other species of the family. The species complex *S. iseri/taeniopterus*, *S. atomarium* and *S. viride* were significantly correlated, and these species were also significantly correlated with site ranking, increasing in abundance toward the west.

DISCUSSION

In many cases, we found that patterns of fish abundance followed expectations based upon habitat distributions, especially distribution of mangroves and seagrass. To this extent, our data support the hypothesis that the presence of appropriate nursery areas near the reefs enhances the abundance of species depending on these nursery areas. However, we also believe that fishing and pollution modified many fish abundance patterns, confounding some of the fish-habitat associations. For example, fishing pressure and pollution levels increased from west to east, whereas lagoonal habitat complexity increased from east to west. This was most evident near Havana City, which has experienced severe overfishing.

The use of mangroves, seagrass beds and/or algal growth in

shallow, near-shore waters has been reported for juveniles *E. striatus* (Dahlgren and Eggleston 2001), *L. apodus* and *S. iseri* (Nagelkerken et al. 2002, Chittaro 2005), *L. cyanopterus* (Heyman et al. 2005), and *S. barracuda* (Nagelkerken et al. 2002). These species showed a significant increase of their abundances in reefs with adjacent seagrass and mangrove habitats that increased in occurrence in western areas of the northern Cuban coast. The mangrove and seagrass beds are very scarce towards the east and near Havana City, but there are always small areas with limited nursery areas for these species, e.g., estuarine mangrove at river mouths and small embayments. Some of these species were present or more abundant near Havana City in the past, but they are targeted and thus have been decimated by overfishing (Aguilar 2005). Grober-Dunsmore et al. (2007) found a very weak relationship of Epinepheline fishes with the associated seagrass surface, but recognized that this was an unexpected result because the current view holds that this group is highly dependent on areas of seagrass. In our case, Epinepheline fishes increased in abundance as habitat complexity within the reef system increased, i.e., in the west.

Cocheret de la Morinière et al. (2002) found that juvenile *A. bahianus* were present mostly in shallow reefs and seagrass areas near these reefs. This species, which settles mostly in shallow waters of the reef and is less dependent on seagrass and mangroves to complete its life cycle, was most abundant in the less complex habitats (eastern area) along the northwestern Cuban coast. In addition, the species may gain some competitive advantage where other important herbivores such as parrotfishes are less abundant.

Parrotfishes are more dependent on the presence of seagrass adjacent to the reef (Dorenbosch et al. 2004, Mumby 2004) and this is particularly true for the most abundant species in the present study, *S. iseri/taeniopterus* (Adams and Ebersole 2002, Cocheret de la Moriniere et al. 2002, Nagelkerken et al. 2002). The pattern showed by this species in our study, with abundance increasing significantly towards the west where there was more seagrass and/or mangroves, agrees with previous research.

We did not predict that *L. synagris* would increase in abundance significantly towards the east. However, *L. synagris* is one of the most important species in the commercial fishery, which takes place in the broad shelf area forming the backreef of Los Colorados reef at the western portion of

our study area. A possible explanation is the species' use of diurnal shelter sites that are mostly patch reefs common in the seagrass beds away from the forereef. Along the eastern portion of our study area, the shelf is narrow with poorly developed or no back reef areas. We believe the species is apparently more abundant in the east because it has no alternative habitat to the forereef and there is less fishing pressure for this species, i.e., spear gun vs commercial fishing by net in the east and west, respectively.

We believe that abundances of large sized species in this study have been affected by high fishing pressure on targeted species (e.g. Aguilar et al. 1997, Aguilar et al. 2004). Aguilar (2005) interviewed local fishermen from Havana City, and they reported the number of species that reach large sizes and

Figure 4. Abundance estimates for species which showed a significant increase in abundance towards the east (upper panel) and towards the west (bottom panels). Species included are those which had significant rank correlations with sites (see Table 2).

were captured frequently in the 1970s have almost entirely disappeared, e.g., *S. guacamaia*, *S. coeruleus*, *S. coelestinus*, *L. maximus*, *Mycteroperca bonaci*, *Epinephelus itajara*, and *Lutjanus jocu*. Only the mutton snapper, *Lutjanus analis*, appears with some abundance during the reproduction time ("runs") and as an effect of some meteorological events (e.g. cold fronts, hurricanes) that cause "arribazones" (fish coming near the shore). Fishermen reported a significant decrease over time in the mean size of individuals observed or captured (e.g., Hutchings 2005). A similar change in fish assemblage composition was reported by Beets et al. (2003) for the Virgin Islands. There, the biomass of large predators appears to be reduced and biomass of herbivores and invertebrate feeders proportionally increased as fishing intensity and other human disturbances increased.

Although there is no formal study on the topic, we assume that there has been a sustained increase in subsistence fishing in the area near Havana City, as a consequence of the economic crisis which started at the beginning of the 1990s. Increasing spear-gun fishing is the main cause of the observed changes into the 1980s, thereafter illicit fishing began with gillnets adding pressure on small and medium size species such as parrotfishes, surgeonfishes and grunts.

Based on our observations reported herein and additional interviews with commercial fishers and tourist fish-

ing operators, increases in fishing pressure are expanding along the entire northwestern coast to the area of Cayo Levisa. Farther west, the human presence is much less and is concentrated in small fishing villages which use mostly commercial fishing gears to target the largest species. In general terms, the main impact of fishing in the entire northwestern Cuban shelf is the reduction of larger fish abundance with the consequence of highly modified fish assemblages along the coast (Aguilar et al. 2004).

Increasing human incursions into coastal ecosystems of the Caribbean most probably intensify the negative impacts on reef fishes. Mumby et al. (2004) report that the parrotfish *S. guacamaia* underwent local extinction during the past 30 years at Glovers Reef, Belize. These authors consider that the extinction of this species at Glovers Reef was most probably due to the removal of its nursery habitat and overfishing. Historical overfishing and mangrove deforestation will certainly work synergistically to reduce herbivory and secondary production at Caribbean coral reef ecosystems (Beets et al. 2003). In our study, the most abundant species were medium-sized herbivores. The removal of large predators and competitors (larger herbivores) by fishermen could allow an increase in the abundance of smaller bodied fishes by competitive release processes.

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